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Modelling carbon and water exchange of a grazed pasture in New Zealand constrained by eddy covariance measurements

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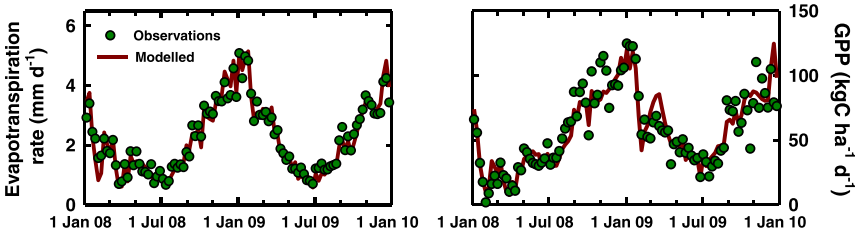
HIGHLIGHTS

- We compared eddy covariance (EC) measurements with process-based modelling.
- Analysis of EC data from grazed pastures was challenging due to grazer respiration.
- Because of intermittant grazing, CO_2 fluxes were temporally and spatially variable.
- Water loss and CO_2 uptake were well modelled—respiration was more problematic.
- Good agreement between modelling and measurements could be achieved.

GRAPHICAL ABSTRACT

Observed and modelled weekly-averaged evapotranspiration rates and gross primary production (GPP) over a grazed pasture in New Zealand.



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ABSTRACT

We used two years of eddy covariance (EC) measurements collected over an intensively grazed dairy pasture to better understand the key drivers of changes in soil organic carbon stocks. Analysing grazing systems with EC measurements poses significant challenges as the respiration from grazing animals can result in large short-term CO_2 fluxes. As paddocks are grazed only periodically, EC observations derive from a mosaic of paddocks with very different exchange rates. This violates the assumptions implicit in the use of EC methodology. To test whether these challenges could be overcome, and to develop a tool for wider scenario testing, we compared EC measurements with simulation runs with the detailed ecosystem model CenW 4.1. Simulations were run separately for 26 paddocks around the EC tower and coupled to a footprint analysis to estimate net fluxes at the EC tower.

Overall, we obtained good agreement between modelled and measured fluxes, especially for the comparison of evapotranspiration rates, with model efficiency of 0.96 for weekly averaged values of the validation data. For net ecosystem productivity (NEP) comparisons, observations were omitted when cattle grazed the paddocks immediately around the tower. With those points omitted, model efficiencies for weekly averaged values of the validation data were 0.78, 0.67 and 0.54 for daytime, night-time and 24-hour NEP, respectively. While not included for model parameterisation, simulated gross primary production also agreed closely with values inferred from eddy covariance measurements (model efficiency of 0.84 for weekly averages). The study confirmed that CenW simulations could adequately model carbon and water

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exchange in grazed pastures. It highlighted the critical role of animal respiration for net CO_2 fluxes, and showed that EC studies of grazed pastures need to consider the best approach of accounting for this important flux to avoid unbalanced accounting.

1. Introduction

Managed grasslands are one of the most important global providers of food and fibre but also have considerable environmental impacts (e.g., Asner et al., 2004; Steinfeld et al., 2006). In New Zealand, dairy farming has become increasingly profitable over recent decades compared with sheep farming or commercial forestry, and it has become the dominant primary industry sector (DairyNZ, 2012). However, dairy farming is also a large contributor to the country's net greenhouse gas emissions, with main contributions from nitrous oxide and methane emissions (MfE, 2014; Kirschbaum et al., 2012).

Additional concern relates to potential losses of soil organic carbon associated with dairy farming. Schipper et al. (2007) analysed archived and newly collected soil samples and reported significant soil carbon losses of 21 ± 18 (95% confidence intervals) tC ha^{-1} over 2–3 decades from flat dairy pastures in New Zealand, while grazed pastures in hill country appeared to have gained similar amounts of carbon as those lost on flat dairy land (Schipper et al., 2010). There are currently no well-substantiated explanations for either of those patterns, but they clearly show that soil carbon stocks under grazed pastures are not inherently steady, but can be significantly modified through management or environmental changes.

The management of farms has been changing over the last few decades, with much greater use of nitrogen fertiliser (Parfitt et al., 2012) leading to higher pasture productivity. This, together with inclusion of increasing amounts of supplemental feed, has allowed higher stocking rates (MacLeod and Moller, 2006; DairyNZ, 2012). Environment conditions are also changing, with gradually rising temperatures (Dean and Stott, 2009) and CO_2 concentrations.

Any of these changes might affect soil carbon stocks, either by affecting carbon inputs from plant productivity or supplemental feed, and/or the rate of decomposition of soil organic carbon, but quantitative information on any changes to rates of input or outputs is lacking. One reason for this relates to the difficulty of accurately quantifying small changes in soil carbon stocks. The inherent variability in soil carbon stocks makes it very challenging to detect soil-carbon changes of less than several tonnes per hectare so that it is difficult to relate any soil-carbon changes to changes in management or environmental factors (e.g., Allen et al., 2010; Arrouays et al., 2012).

However, small changes in ecosystem carbon stocks can be inferred over short time intervals using eddy covariance (EC) measurements of net ecosystem CO_2 exchange (e.g., Baldocchi, 2003). When measurements of daily carbon exchange are combined with estimates of other carbon fluxes to and from the farm system, it becomes possible to deduce overall net ecosystem carbon balances and changes in soil carbon stocks.

The main CO_2 fluxes are photosynthesis (or gross primary production, GPP) and respiration, consisting of autotrophic (plant) respiration, heterotrophic respiration by decomposer organisms, and animal respiration when pastures are being grazed. GPP minus respiration gives net ecosystem production (NEP), the flux that can be measured by EC techniques. In this paper, we follow the convention of Chapin et al. (2006), with positive values of NEP indicating net carbon uptake by the ecosystem.

In grazed pastures, any positive NEP is largely balanced by the export of carbon in milk products and methane emission by ruminant animals, but small imbalances can remain to imply either gains or losses of soil organic carbon (Soussana et al., 2010). Additional important carbon fluxes are supplemental feed provision and harvesting for silage, which may be transported outside the area under study, or fed back to animals on the same paddocks but at a different time. Other carbon fluxes, such as those linked to erosion, fire, leaching of dissolved organic matter, lateral transport by wind or animals, and fluxes by methane and non-methane volatile organic carbon emissions all contribute to the overall carbon budget, with their importance varying with the properties of particular systems (Chapin et al., 2006).

A world-wide network of flux stations has now been developed with over 500 individual sites (http://fluxnet.ornl.gov/) to cover a wide variety of ecosystem types. Most EC systems have been deployed over natural vegetation, while grazed pastures have been studied less often. This imbalance is gradually receding as a number of studies of grazed pastures have been published more recently (e.g., Zeeman et al., 2010; Klumpp et al., 2011; Peichl et al., 2012; Leahy and Kiely, 2012; Wohlfahrt et al., 2012). However, there is still only limited experience with the study of grazed pastures that have to deal with the particular challenge of having small, but continuous, fluxes from GPP and plant and soil respiration that are occasionally punctuated by much larger fluxes from animal respiration during grazing events.

For the EC technique to give reliable estimates of surface–atmosphere exchange of scalars, meteorological conditions have to conform to certain assumptions. The most important of these are adequate turbulence, a mean vertical windspeed of zero, and the absence of any advective flows (Kaimal and Finnigan, 1994; Foken et al., 2004; Göckede et al., 2004; van Gorsel et al., 2008). The analysis also relies on steady-state fluxes that can be averaged over typical integration periods of 15 or 30 min (Finnigan et al., 2003). Farms, however, often consist of a mosaic of individually managed paddocks, which introduces spatial and temporal heterogeneity to the flux footprint (Peichl et al., 2010; Wohlfahrt et al., 2012). Horizontal heterogeneity of the surface could be caused, for example, by adjacent fields growing different crops, or paddocks being in different stages of recovery after grazing or cutting.

At an intensively grazed dairy farm, rotational grazing of paddocks is the main cause of spatial and temporal heterogeneity caused by "temporal asynchrony of management practices" (Wohlfahrt et al., 2012). While cows are grazing a paddock, around 50% of ingested carbon is respired (Soussana et al., 2004; Zeeman et al., 2010), causing the grazed paddock to become a potentially large temporary net source of CO_2, while the surrounding paddocks are likely to remain sinks for CO_2. Fertiliser application is also often linked to grazing (e.g., Peichl et al., 2012), adding further to spatial heterogeneity. This heterogeneity essentially violates the assumptions underpinning the application of EC techniques, causing data quality to decrease (Rannik et al., 2012). So, even dairy farms that are aerodynamically fairly uniform can thus be heterogeneous in terms of the fluxes of CO_2, and sensible and latent heat.

Previous EC studies have adopted different approaches to deal with data analysis when there was grazer respiration in (part of) their flux footprint. Some studies assumed EC flux measurements to include animal grazing (e.g., Nieveen et al., 2005; Jaksic et al., 2006; Byrne et al., 2007; Soussana et al., 2007). Others cautioned against the use of data collected during grazing events (Zeeman et al., 2010; Baldocchi et al., 2011), and others intentionally discarded data collected during grazing events (e.g., Skinner, 2008).

Despite the challenges posed by spatial and temporal heterogeneity, EC measurements are still one of the best tools available to measure net CO_2 exchange in grazed pasture systems. Coupling EC data with measurements or estimates of other non-CO_2 carbon fluxes into and out of the system (e.g., milk, methane, silage import/export), allows the full carbon balance of a site to be determined over short time intervals. Mudge et al. (2011) previously used this approach and concluded that

the site was a carbon sink during both years of measurement. In the current study, we used the data from Mudge et al. (2011) to calibrate the detailed ecosystem carbon model CenW (e.g., Kirschbaum, 1999; Kirschbaum et al., 2003) to provide a better quantification and understanding of the temporal patterns of NEP in this system.

Specifically, the present work aimed to

1) use EC measurements to parameterise CenW to provide 2 years of matching simulations; and
2) test whether we could identify potential biases in EC measurements due to undetected fluxes from sporadic grazing events.

Our overall aim was to develop CenW to accurately model the water and CO_2 fluxes of this grazed pasture system to allow future testing of alternative scenarios of either management or climatic changes to identify possible management options that could maximise soil carbon stocks.

2. Materials and methods

2.1. Experimental details

Details of the experimental design, site, and measurement routines have been provided by Mudge et al. (2011), and they are only briefly repeated here. The experimental site was situated on a grazed dairy farm (Fig. 1), located near Hamilton, North Island of New Zealand, at 37.46°S 175.22°E. The study commenced in January 2008, and we used two years of continuous measurements of NEP observed with an EC tower to parameterise our model.

2.1.1. Site and farm management information

The paddocks were predominantly covered with perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*), the species that typically dominate New Zealand's pastoral systems. The site is an experimental dairy farm operated by DairyNZ, which uses the farm for various farm system trials, with different sets of paddocks used for different trials with different experimental protocols. Detailed records were kept of the grazing, supplementary feeding and harvesting carried out on each paddock.

Cattle typically graze for 12 months of the year in small herds (usually 9–21 cows) on mini-paddocks that are mostly 0.5 ha (50 × 100 m) in size (Fig. 1). Although paddock and herd sizes on this research farm were smaller than on typical commercial farms, the overall stocking rate (~3 cows per ha) and management regimes were similar. Individual paddocks were grazed on different schedules as required to meet the specific objectives of different research questions. Grazing events were mostly restricted to single days, but extended over several days on other occasions. For some periods, grass was also cut and removed offsite for indoor grazing. These different events were explicitly included in the CenW simulations.

Taken as a whole, the EC measurements on the farm were thus representative of a typical whole-farm system. Cattle typically grazed in multiple small herds on different paddocks, with some paddocks within the flux footprint being grazed on most days. The average grazer respiration from the footprint area was thus more even and reached lesser extremes than it would have reached if only one large herd had been grazing the whole footprint area. However, with the small paddock and herd sizes, it led to considerable heterogeneity within the study area. On particular days, some paddocks within the footprint area were likely to be grazed while others would have been regrowing after recent grazing, or contained high biomass if the previous grazing event was more distant. This site, therefore, proved to be particularly challenging for EC analyses.

2.1.2. CO_2 flux measurements and data processing

CO_2 fluxes were measured using the instrument setup described in Mudge et al. (2011). However, because some changes were made to the data screening procedure, full details are given below. CO_2 flux data were rejected at times of:

i) unreliable data from the IRGA or the sonic anemometer as indicated by warnings from these sensors;
ii) unreliable readings from the LI-7500 (LI-COR Inc., Lincoln, NE, USA) CO_2 analyser as indicated by a deviation of the automated gain control (AGC) signal from the 'baseline', resulting, for example, from rain or fog;
iii) out-of-range fluxes ($|NEP| > 50$ μmol m^{-2} s^{-1});
iv) lack of stationarity in the high frequency CO_2 concentration time series indicated by large standard deviation in CO_2 density (>15 mg m^{-3} during the day, and >30 mg m^{-3} at night);
v) low friction velocity (<0.11 m s^{-1});
vi) large deviation of flux values from the mean computed for the appropriate time of day across a 20-day moving windows [when flux exceeded a threshold number of standard deviations (night-time = 4, daytime = 3) from the mean flux].

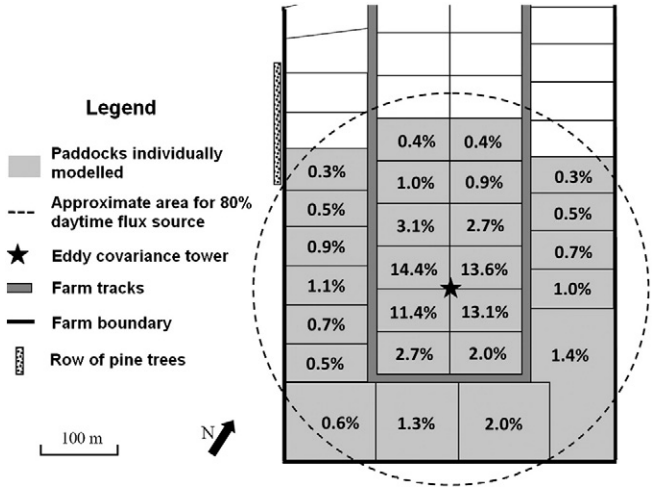

Fig. 1. Layout of the experimental site with the paddocks around the EC tower. Each rectangle represents the outline of a different paddock. The dashed circle shows the approximate distance within which more than 80% of fluxes were sourced. We individually modelled the gas exchange of each paddock shown in grey. Numbers in the figure indicate the average flux sourced from each different paddock according to the footprint model.

Gaps in NEP were filled and NEP partitioned between GPP and total ecosystem respiration rate (TER) using the online gap-filling and flux partitioning procedure described by Reichstein et al. (2005). This gap-filling model is an improved, sliding-window look-up table that utilises both the covariation of NEP with meteorological conditions and temporal autocorrelation of NEP (Moffat et al., 2007). In the Reichstein et al. (2005) routine, TER was modelled using the Lloyd and Taylor equation (Lloyd and Taylor, 1994) fitted to soil temperature. Following this approach, night-time TER was first regressed against night-time soil temperature, and this relationship was then used to estimate TER for both night-time and daytime. GPP was determined by subtracting the modelled TER from NEP.

2.2. Modelling details

CenW (Carbon, Energy, Nutrients, Water) is a process-based model, combining the major carbon, energy, nutrient and water fluxes in an ecosystem as shown in Fig. 2 (Kirschbaum, 1999). The model combines these fluxes to simulate the carbon balance of a system over time. CenW has been extensively used and tested for *Pinus radiata* (e.g., Kirschbaum, 1999; Kirschbaum and Watt, 2011) and *Eucalyptus delegatensis* forests (Kirschbaum et al., 2007), and to a

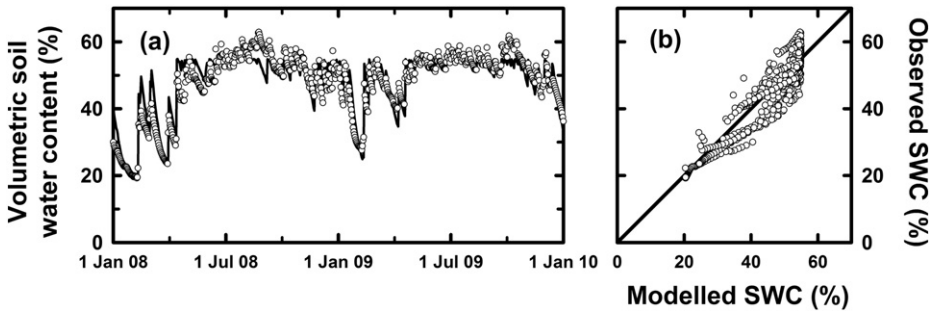

Fig. 2. Time course of measured (symbols) and modelled (solid line) volumetric soil water contents (a) and observed vs modelled values (b). Model efficiency for the comparisons was 0.86.

lesser extent for grasslands (e.g., Kirschbaum et al., 2003). The soil organic matter component of the model is based on the CENTURY model (Parton et al., 1987), which was originally developed for grasslands.

The model runs on a daily time step. Major ecosystem processes are photosynthetic carbon gain by plants and losses through both autotrophic plant respiration and heterotrophic respiration by soil organisms and grazing animals. These fluxes are modified by temperature, and nutrient and water balances. The model contains a fully integrated nitrogen cycle, but with frequent pasture fertilisation at the experimental site, it was likely that nutrient levels posed only minor constraints on productivity.

The model also contains a fully-coupled water cycle, and it is likely that soil water availability constituted an important constraint on plant productivity over the summer months at the experimental site. Water is gained by rainfall and lost through evapotranspiration. Any amount of water exceeding the soil's water-holding capacity is lost by deep drainage beyond the root zone, with important controls by soil depth and water-holding capacity. Total evapotranspiration is modelled by separately modelling the contributions from canopy evaporation, soil evaporation, and plant transpiration. These individual fluxes are calculated using the Penman–Monteith equation, with canopy resistance for calculating transpiration explicitly linked to photosynthetic carbon gain.

For the present work, we used CenW version 4.1, which is available, together with its source code and a list of relevant equations, from http://www.kirschbaum.id.au/Welcome_Page.htm. A number of additional routines were added for the present work, and they have been described in Appendix A. A list of relevant parameters is given in Appendix B.

To model NEP effectively in a grazed pasture system, it was essential to know the timing of grazing, feed supplementation and harvesting carried out on each paddock. The model assumed that cows consumed 55% of available foliage (Pal et al., 2012) at each grazing event. If grazing was spread over several consecutive days, grazing percentages on individual days were adjusted to add to a total of 55%. Of that feed, 50% was assumed to be lost by respiration (Zeeman et al., 2010), 5% as methane (Kelliher and Clark, 2010), and 18% removed as milk solids (Crush et al., 1992; Soussana et al., 2010; Zeeman et al., 2010), with the remaining 27% returned to the paddock in dung and urine. Animal weights were assumed to remain constant and not add to carbon gains or losses from the paddocks.

As the footprint of the EC tower covered different paddocks at different times, we modelled the CO_2 and water exchange separately for each of 26 different paddocks surrounding the tower (shaded boxes in Fig. 1), using daily records of grazing, harvesting and supplemental feed provision for each paddock as inputs. We combined the modelled gas exchange with a modelled source distribution of fluxes at respective times, and compared that integrated net flux with observed fluxes recorded at the tower.

A notional 27th paddock was modelled as a generic paddock to cover the gas exchange flux originating from paddocks that were further away from the EC tower. For this generic paddock, a regular daily grazing intensity of 1.5% of foliage was assumed as we had no information on the actual grazing times on those paddocks. Model outcomes were fairly insensitive to the setting of that grazing intensity (data not shown).

A half-hourly footprint analysis was conducted for the source area of the fluxes measured at the tower using the Kormann and Meixner (2001) footprint model. Half-hourly CO_2 and H_2O fluxes were then averaged to daily values for days when the footprint could be calculated, or on a few days with missing wind information, the footprint information from the previous day was re-used. Modelled gas exchange from each paddock was then multiplied by the proportion of gas exchange originating from respective paddocks (as calculated by the footprint model for each day). Average flux weighting for each paddock is shown in Fig. 1. These weighted fluxes then provided the modelled fluxes that were compared with the fluxes measured at the tower.

2.3. Additional climate data

During the measurement period, the weather data required for model simulations (daily minimum and maximum temperatures, rainfall, solar radiation, and absolute humidity) were available from a meteorological station maintained at the EC tower, but the tower provided no information for the period before the start of measurements in 2008. In order to provide realistic initial conditions, the model was run for 4 years before the start of the experimental period with weather data obtained from a nearby weather station (Ruakura, 37.78°S 175.32°E; situated 6.4 km from the EC tower). Slight differences between the sites were identified by comparing measured values on corresponding days over 2 years, and the Ruakura data were corrected for these differences before being used.

2.4. Ancillary measurements

Most of the EC footprint area was underlain by a silt-loam surface horizon and subsoil. Soil water near the tower was measured half-hourly (CS616, Campbell Scientific, Logan, UT) at 50 and 100 mm depths. The model was run with a separation into six soil layers, spanning depths from 0–25, 25–50, 50–100, 100–200, 200–300, 300–500, and 500–700 mm. The top soil was reported to have a water-holding capacity of 43% (v/v; Mudge et al., 2011), which was modified to 38% in the model runs through detailed comparison between measured and modelled soil water contents over the experimental period. During most of 2008, total above-ground pasture biomass of most paddocks was quantified weekly by DairyNZ staff using the visual assessment method of Piggot (1989) that was recalibrated during each weekly reading.

2.5. Parameter estimation and statistical analysis

The model was optimised by selecting parameter values that minimised the residual sums of squares across different EC measurements and ancillary observations. Measurements used for comparison were daily and weekly-averaged estimates of evapotranspiration and biomass estimates that were available for most paddocks over the first year of the experiment. We also used daily and weekly-averaged estimates of daytime, night-time and 24-hour NEP. However, grazing events disproportionately affected modelled and measured rates of NEP, especially night-time NEP, and we excluded periods (5% of data) with largest grazer respiration from the 4 paddocks surrounding the EC tower.

We separated our two years of eddy covariance data into weekly sets, with the first set used for parameter optimisation and the second set for model validation. For biomass data, we included half the measured paddocks for parameter optimisation and the other half for model validation. CenW has an automatic parameter optimisation routine that varied parameter values within specified limits with the aim of minimising the residual sums of squares of both daily and weekly-averaged data.

The overall goodness of fit was described by model efficiency (*EF*), which was determined as (Nash and Sutcliffe, 1970):

$$EF = 1 - \frac{\sum (y_o - y_m)^2}{\sum (y_o - \overline{y})^2}$$

where y_o are the individual observations, y_m the corresponding modelled values and $\overline{y}$ the mean of all observations.

This statistical measure quantifies both tightness of the relationship between measured and modelled data and assesses whether there is any consistent bias in the model. High model efficiency can only be achieved when there is a tight relationship with little unexplained random variation and little systematic bias. The final set of parameter values is given in Appendix B.

3. Results and discussion

Short dry periods during summer are relatively common in this region, but the length and extent of water shortage in 2008 were unprecedented (i.e., described as a 1 in 100-year drought). Rains returned in April 2008, and the remainder of the year was quite mild, with good growing conditions. There was a shorter period of summer drought in 2008/2009, followed by a relatively cool winter (Mudge et al., 2011). It thus provided a range of environmental conditions as a good basis for fitting model parameters.

3.1. Overall model performance

Overall, there was good correspondence between modelled and observed data (Table 1). Agreement was particularly good for evapotranspiration, with model efficiencies of 0.91 and 0.96, for daily and weekly comparisons of the validation data set. This indicated good simulation of the seasonal cycle, including the effect of drought conditions.

For the different measures of CO_2 exchange, data quality was uncertain for days when cows were grazing on the paddocks immediately around the EC tower. These issues are further illustrated and discussed below. We therefore excluded periods with grazing on the inner four paddocks around the tower when the footprint analysis indicated that fluxes from those paddocks should have reached the tower (5% of observations). With exclusion of these data, agreement was quite good, with model efficiencies for weekly averaged data of the validation set for 24-hour, daytime and night-time NEP of 0.54, 0.78, 0.67 respectively (Table 1). Modelled mean foliage mass was also fairly consistent with observations, with a model efficiency of 0.58.

Soil water was also compared against observations, but with measurements at only a single location, we could not be certain that these measurements were necessarily representative for the whole paddock, and they were therefore not included for formal model optimisation. However, good agreement was nonetheless achieved, with model efficiencies of 0.86 and 0.80 for observations at 5 and 10 cm, respectively.

We did not formally include GPP and TER for model optimisation as the values estimated from eddy covariance measurements could not include the irregular and episodic nature of grazing events. This issue is further illustrated and discussed below. However, despite not formally being optimised, EC-derived GPP estimates agreed very closely with CenW estimates, with model efficiency for weekly estimates of 0.84. Estimates of TER also agreed well for weekly comparisons, with a model efficiency of 0.84, but agreement was much poorer for daily comparisons, with model efficiency of only 0.63. This difference is largely attributable to the non-capture of grazing events in the eddy covariance derived TER estimates, which greatly affected daily values, but was largely averaged out at weekly intervals.

It was thus possible to provide a useful quantification of this important component of the overall carbon balance of the site. The

Table 1
Summary of mean observed and modelled data available in the experiment, and model efficiencies of the fit between modelled and observed data. For NEP measures, data were excluded when grazing on the four inner paddocks around the tower were considered to have added a large respiratory flux. Foliage-mass data were only available for 2008.

	Observed	Modelled	Model efficiency			
			Parameterisation		Validation	
	Average values over two years		Daily	Weekly	Daily	Weekly
24-hour NEP	5.1 kgC ha^{-1} d^{-1}	3.2 kgC ha^{-1} d^{-1}	0.50	0.58	0.56	0.54
Daytime NEP	31.0 kgC ha^{-1} d^{-1}	29.6 kgC ha^{-1} d^{-1}	0.65	0.72	0.71	0.78
Night-time NEP	−25.9 kgC ha^{-1} d^{-1}	−26.4 kgC ha^{-1} d^{-1}	0.57	0.81	0.43	0.67
GPP	57.9 kgC ha^{-1} d^{-1}	58.4 kgC ha^{-1} d^{-1}			0.79	0.84
Total respiration	52.9 kgC ha^{-1} d^{-1}	53.3 kgC ha^{-1} d^{-1}			0.63	0.84
Evapotranspiration rate	2.24 mm d^{-1}	2.21 mm d^{-1}	0.91	0.95	0.91	0.96
Soil water (5 cm)	47.8%	48.5%			0.86	
Soil water (10 cm)	47.2%	45.8%			0.80	
Foliage biomass	1.04 tC ha^{-1}	1.04 tC ha^{-1}	0.57			0.58
				Final model estimates (averaged over two years)		
GPP				58.4 kgC ha^{-1} d^{-1} (21.3 tC ha^{-1} yr^{-1})		
Autotrophic respiration				34.1 kgC ha^{-1} d^{-1} (12.5 tC ha^{-1} yr^{-1})		
Heterotrophic soil respiration				12.9 kgC ha^{-1} d^{-1} (4.7 tC ha^{-1} yr^{-1})		
Grazer respiration				6.7 kgC ha^{-1} d^{-1} (2.5 tC ha^{-1} yr^{-1})		
Milk export				2.4 kgC ha^{-1} d^{-1} (0.89 tC ha^{-1} yr^{-1})		
Methane emission				0.67 kgC ha^{-1} d^{-1} (0.25 tC ha^{-1} yr^{-1})		

simulations indicated that the site fixed about 21.3 tC ha^{-1} yr^{-1} in GPP (Table 1). Of that, approximately half (12.5 tC ha^{-1} yr^{-1}) was lost in autotrophic respiration and a further 4.7 tC ha^{-1} yr^{-1} in heterotrophic soil respiration. Cattle respiration added a further respiratory flux of 2.5 tC ha^{-1} yr^{-1}, about half the respiratory flux by soil heterotrophs. A further 0.89 tC ha^{-1} yr^{-1} was exported in milk solids and 0.25 tC ha^{-1} yr^{-1} was lost through methane emissions.

3.2. Soil moisture and evapotranspiration

Soil water contents at 50 mm were well modelled, with a model efficiency of 0.86 and good agreement between modelled and observed on average water contents (Table 1; Fig. 2). Some of the remaining discrepancies were due to measured water contents being above the soil's identified water-holding capacity. This probably reflected incomplete drainage and some ponding during very wet periods. Conversely, observed soil water contents were sometimes lower than modelled values during rewetting after drought periods. This was probably due to some cracks developing in the soil that allowed water to bypass the 50-mm layer and directly rewetted deeper soil layers.

The good agreement between observed and modelled soil water contents was consistent with the very good modelling of evapotranspiration rates (Fig. 3). The model replicated the seasonal cycle over 2 years, including the interaction between seasonal and plant factors as well as short-term phenomena, such as responses to day-to-day changes in weather patterns. Evapotranspiration ranged from minima of less than 1 mm d^{-1} in winter to peaks in weekly averages of about 5 mm d^{-1} in summer. Evapotranspiration rates during the 2008 drought were similar to values in the middle of winter. Low rates in winter were due to low net radiation and vapour pressure deficits, and low rates during the drought were due to stomatal closure that limited rates of transpiration, while a dry canopy and soil surface prevented canopy and soil evaporation.

3.3. CO_2 exchange

3.3.1. Ecosystem respiration—challenges posed by grazing events

One of the key challenges of measuring NEP in intensively grazed pastures lies in the capture of animal respiration during grazing events. Their importance is illustrated for a representative period in Fig. 4, which shows modelled grazer respiration for the average of all modelled paddocks and for the four paddocks immediately around the tower (Fig. 4a) and modelled TER (Fig. 4b).

This illustrates the large fluxes that can result from grazing events and their discrete timing. During a grazing event, cows can graze paddocks from a pre-grazing pasture cover of up to 3000 kgDW ha^{-1} and ingest up to 1650 kgDW ha^{-1} (assuming 55% of available feed being ingested; Pal et al., 2012). Assuming a carbon content of 50%, this equates to an intake of up to 825 kgC ha^{-1} d^{-1}. We assumed that

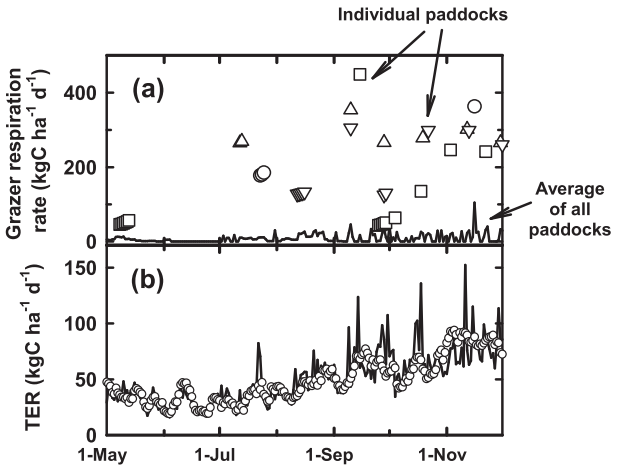

Fig. 4. Grazer and total respiration shown as an example for the period from 1 May to 1 December 2009. Panel (a) shows CenW-modelled grazer respiration rates from the four paddocks closest to the EC tower (with different paddocks shown by different symbols) and the average rate of grazer respiration of all 26 modelled paddocks (solid line). Panel (b) shows total ecosystem respiration (TER) rates calculated with an EC-based model (Reichstein et al., 2005) shown by symbols, and those calculated with CenW (solid line) for fluxes at the tower (b). The spikes in (b) occurred on days when there were grazing events and when a large part of the CO_2 flux at the tower was sourced from grazed paddocks.

cows respired 50% of their ingested uptake (Zeeman et al., 2010) to equal a maximum respiration rate of about 400 kgC ha^{-1} d^{-1}.

In practice, modelled daily respiration rates were usually less than the maximum estimate (Fig. 4a). Sometimes, modelled biomass did not quite reach the targeted threshold of 3000 kgDW ha^{-1}, especially when consecutive grazing events were spaced fairly closely together. This led to smaller respiratory fluxes from cows because less biomass was consumed. In addition, paddocks were also often grazed over several consecutive days, and we had to assume that cows removed similar amounts on each of these days. Nonetheless, on many occasions, grazer respiration could substantially exceed typical respiration rates from autotrophic plant respiration and soil heterotrophic respiration (Fig. 4b).

There was limited grazing over the winter months, especially in June, and over that period, there was close agreement between the CenW (solid line in Fig. 4b) and EC-based estimates (symbols in Fig. 4b) of respiration rates. The very high spikes in respiration rates modelled by CenW from July onwards corresponded to days when there were large grazing events that should have been observed at the EC tower based on the footprint analysis. Most of these spikes in grazer respiration rates (Fig. 4b) coincided with grazing on the four paddocks around the tower (Fig. 4a), but that was not always the case. Some of the grazing events shown in Fig. 4a were not observed at the tower because of the wind direction on those days. Conversely, some of the

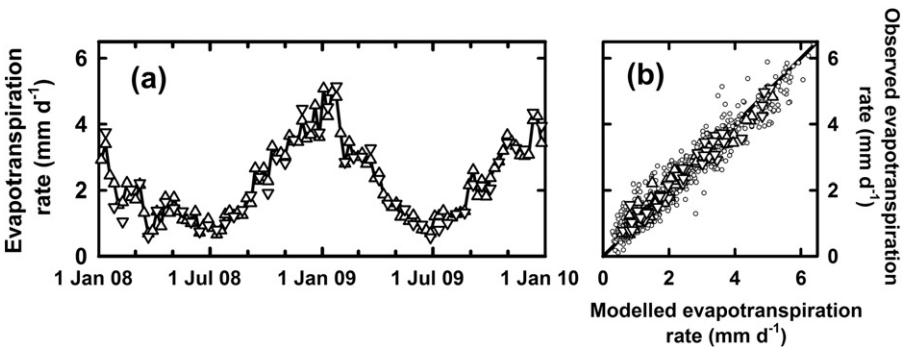

Fig. 3. Time course of measured (symbols) and modelled (solid line) weekly-averaged evapotranspiration rates (a), and observed vs modelled daily and weekly-averaged rates (b). Daily rates are shown with smaller symbols and weekly averaged rates larger with larger symbols. The data from the calibration set are shown with up-arrows and the validation set with down-arrows. Model efficiencies for daily and weekly comparisons for the validation set were 0.91 and 0.96, respectively.

smaller respiration peaks shown in Fig. 4b were not related to grazing of the inner paddocks, but originated from some of the outer paddocks.

The EC based TER estimates had none of those large peaks (Fig. 4b). The Reichstein et al. (2005) partitioning routine modelled TER as a function of soil temperature based on all valid night-time NEP measurements over a moving window of observations. As it had no information about grazing in the footprint area, it could not distinguish between plant and soil respiration, on the one hand, and animal respiration on the other. Instead, any measured grazer respiration had to be subsumed into the total respiratory flux. CenW, on the other hand, allowed explicit modelling of autotrophic plant and heterotrophic soil respiration rates based on biophysical constraints, and grazer respiration based on grazing records.

While the EC-based respiration model did not have any large peaks, it instead gave higher average respiration rates than the rates modelled for plant and soil-heterotrophic respiration by CenW. These slightly inflated estimates of TER by the EC-based model were most notable in late September and around 1 November (Fig. 4b). Over those periods, the average EC-based respiration estimates were similar to the CenW estimates that included all respiration components, but the EC-based estimates gave relatively smooth rates compared to the more irregular nature of CenW-based estimates that reflected the presence of cows on particular days in the tower footprint.

The difference between the two TER estimates was also reflected in a direct comparison of respiration rates (Fig. 5). At lower TERs, there was good agreement between the two estimates, and all data nestled around the 1:1 line. These data were mainly obtained over winter when there was minimal grazing. At higher respiration rates, however, the values started to diverge and showed little correlation with each other. In particular, CenW often modelled high respiration rates during grazing events, which were not apparent in the EC-based respiration estimates.

At other times, the EC-based TER estimates were higher than those calculated by CenW. This corresponded to days without grazing events when CenW modelled respiration without a grazer contribution, whereas the gap-filled EC-based estimates had been elevated by grazer respiration in the days before and after those specific days (cf. the September and November periods in Fig. 4b). The EC-based estimates could not distinguish between grazer and other respiration and thus could only generate generic empirical respiration estimates that included all contributions. The EC-based modelled rates consequently resulted in a fairly smooth rate, with variance driven only by environmental factors. CenW, on the other hand, modelled a smooth lower rate corresponding to plant and soil heterotrophic respiration that was occasionally punctuated by spikes from grazer respiration.

On average, both methods derived similar TER estimates, with 52.9 kgC ha^{-1} d^{-1} for EC based estimates while CenW modelled an average of 53.3 kgC ha^{-1} d^{-1} (Table 1). Despite the problems outlined here, there was still a high correlation between the two respiration estimates, with model efficiencies for daily and weekly comparisons of 0.63 and 0.84. The disparity between daily and weekly model efficiencies reflects the importance of grazing events that would have greatly affected daily comparisons but would have been averaged out over weekly integration intervals, resulting in much higher model efficiency.

The challenge of comparing observed and modelled NEP is further illustrated in Fig. 6, which shows all observed vs modelled night-time NEP data, separated into the 95% of data without grazing recorded for the four inner paddocks around the tower (open symbols) and 5% of data with grazing on the inner paddocks when the footprint model suggested that the flux should have reached the EC tower (closed symbols). The data without grazing were well correlated between model and observations. However, some of the data with grazing deviated strongly from the 1:1 line, particularly showing large modelled NEP between −40 and −60 kgC ha^{-1} d^{-1} when the observations showed NEP of only −20 to −40 kgC ha^{-1} d^{-1} (Fig. 6). A similar pattern was not apparent for daytime fluxes (data not shown).

While the 1:1 line gave a good description of the correlation between the two data sets for days without grazing, a line fitted to the data including nights with grazing events resulted in a strong deviation from the 1:1 line (shown by the dashed line) and a slope of only 0.65. It indicates that uncritical use of all available data would have created a significant bias in the data fit, resulting in biased parameter estimation. The discrepancy between modelled and observed fluxes could have been caused by large emissions not appearing in the observations because they would have been discarded by the data-quality filters. It could have also been caused by errors in the flux footprint calculations that might have erroneously predicted that a large respiratory grazing efflux should have been observed by the tower, whereas in reality, the emission might have by-passed detection at the tower.

3.3.2. Dealing with between-paddock variability

In the present work, we modelled fluxes from each paddock individually using CenW and combined those fluxes to generate integrated CO_2 and water fluxes that would be expected to be observed at the EC tower. Here, we explore the effect of that approach. Fig. 8 compares NEP integrated with the Kormann–Meixner footprint model with calculated rates either using the average of all 26 paddocks (Fig. 7a) or rates

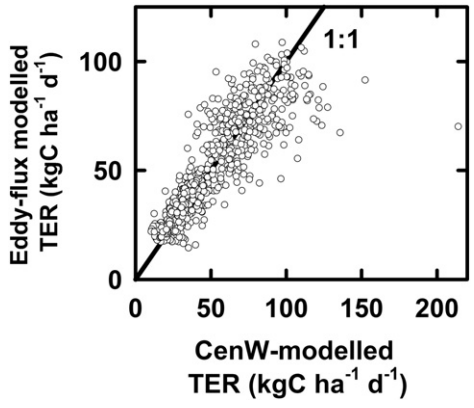

Fig. 5. Total ecosystem respiration rate (TER) for all individual days modelled with the EC-based model plotted against CenW-simulated data. The 1:1 line is also shown. The average of EC-based modelled respiration was 52.9 kgC ha^{-1} d^{-1}, while the CenW modelled average was 53.3 kgC ha^{-1} d^{-1}.

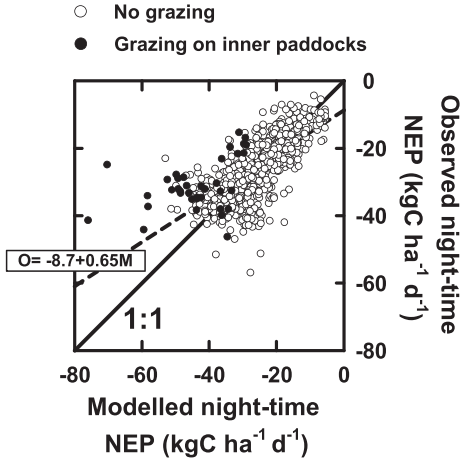

Fig. 6. Apparent errors introduced by incomplete capture of grazing events. Data show night-time modelled and observed NEP, identified as the data obtained without gazing on the four inner paddocks (open symbols) and a number of observations with grazer respiration on the inner paddocks with wind directions indicating that it should have reached the tower (closed symbols). The dashed lines were fitted to all data, with parameters shown in the figure. Also shown is a 1:1 line.

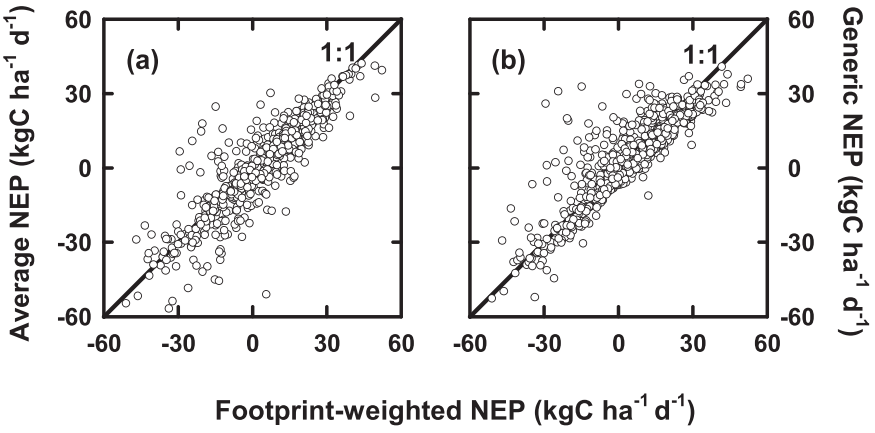

Fig. 7. Modelled 24-h NEP calculated as the average of all modelled paddocks (a) and the simulations of a generic paddock with continuous daily grazing (b) plotted against NEP weighted by the flux footprint model. The lines are 1:1 lines. Lines of best fit fitted have r^2 of 0.79 (in a) and 0.75 (in b) of the variation.

calculated from a generic paddock with a continuous small amount of daily grazing (Fig. 7b). For the comparison of average and footprint-weighted rates, the underlying rates for each of the 26 paddocks were identical, with the only difference being their integration either by a simple average or through the footprint model that explicitly accounted for differences in wind patterns on different days.

The comparison between averaged and footprint-weighted rates shows many days with rates nestled close to the 1:1 line, but a large number of days with rates substantially deviating from each other without forming any distinct patterns. These points corresponded to days with large grazing events that were either amplified in the footprint-weighted data because the flux on those days originated from the grazed paddocks, or were dampened because the flux originated from ungrazed paddocks. Overall, the correlation between the data sets had an r^2 of 0.75, which means that different integration options alone introduced 25% variation into the data sets.

In the comparison between footprint-weighted and generic simulations (Fig. 7b), there was a similar level of variance ($r^2 = 0.72$), but it displayed some distinct patterns. The majority of data points lay slightly below the 1:1 line, corresponding to days without grazing on paddocks where the flux originated from, while the generic modelling still had to assume some on-going regular grazing that led to slight CO_2 losses that lowered rates on those days. Conversely, there were a smaller number of days when fluxes based on the footprint weighting were much lower than the 1:1 line (displaced to the left). These days corresponded to days when significant fluxes originated from grazed paddocks.

Further analyses showed that GPP and evapotranspiration were highly correlated between averaged and footprint-weighted fluxes, while the correlation was significantly lower for respiration fluxes (Table 2). It showed that the importance of correctly sourcing the fluxes was essentially determined by the episodic and quantitatively important grazing fluxes. GPP and evapotranspiration fluxes also differed significantly between paddocks depending on the time since grazing (data not shown), but these differences were much smaller than the respiratory differences between grazed and ungrazed paddocks. There were also usually several paddocks at various stages of post-grazing recovery so that differences in the comparison between combined rates were barely noticeable. Differences in grazer respiration rates, on the other hand, were both large and often restricted to one or two specific paddocks so as to show up much more strongly in the comparisons.

Using footprint-weighted rather than simply averaged fluxes to compare with observations improved model efficiencies by about 10% from 0.39 to 0.52 for 24-hour NEP, 0.60 to 0.69 for daytime NEP and 0.37 to 0.50 for night-time NEP (Table 2), indicating that use of the footprint-weighting methods could usefully account for some of the existing variation between paddock. The size of the improvement by 10% (or 20% of remaining variation) was limited by the number of observations that could be improved through better matching of observed and modelled fluxes. As significant differences between averaged and footprint-weighted rates were only apparent for grazer respiration, improvements in model efficiency were restricted to days with significant grazer fluxes but made little difference when there was no grazing activity.

Table 2
Comparison between observed and modelled data if modelled data were taken as the simple average of all modelled paddocks or weighted by the footprint model.

	Correlation between averaged and weighted	Model efficiency for comparison against observations		
		Averaged	Weighted	Generic
24-hour NEP	0.79	0.39	0.52	0.44
Daytime NEP	0.87	0.60	0.69	0.63
Night-time NEP	0.82	0.37	0.50	0.48
GPP	0.994			
Total respiration	0.868			
Evapotranspiration rate	0.9988			

The first column simply gives the correlation coefficient (r^2) when daily values of averaged and footprint weighted data are plotted against each other. The next three columns compare model efficiencies for modelled data compared against observations, when modelled data used the average of rates from all paddocks, the footprint-weighted average or rates from a generic paddock that was modelled with a continuous low daily grazing rate.

3.3.3. Net ecosystem productivity

The outliers with much higher modelled than observed CO_2 emission rates (Fig. 6) could have caused important biases in the parameter fitting. Further analyses and model parameterisation therefore only used data from days without significant grazer respiration from the four paddocks around the tower.

NEP showed relatively little seasonality, with the patterns of changes instead dominated by short-term weather patterns such as droughts in both summers in the analysis period, and during weeks of unfavourable weather in any season (Fig. 8). Highest NEP of about 30 kgC ha^{-1} d^{-1} was observed during favourable weather in summer but was only slightly higher than NEP during favourable weeks in the middle of winter, and lowest values of about 10 kgC ha^{-1} d^{-1} were seen during drought periods. The muted seasonal pattern for NEP hides the fact that the underlying carbon gains (Fig. 9) and losses (data not shown) were much higher during the summer than winter months, but the higher rates of gains and losses negated each other for little remaining seasonal patterns.

Model efficiencies were 0.56 and 0.54 for daily and weekly 24-hour NEP comparisons, respectively. Daytime NEP alone showed better agreement between modelled and observed values, with model

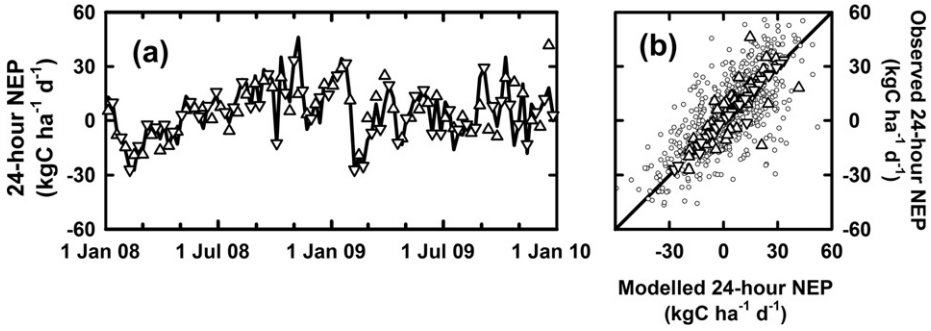

Fig. 8. Time course of measured (symbols) and modelled (solid line) 24-hour NEP (a), and daily and weekly-averaged data plotted against each other (b). Model efficiencies of the validation data set for daily and weekly comparisons were 0.56 and 0.54, respectively. Symbols as for Fig. 3.

efficiencies of 0.71 and 0.78 for daily and weekly comparisons, and night-time NEP had model efficiencies of 0.43 and 0.67 (Table 1).

3.3.4. Gross primary production

Even though CenW was not explicitly optimised using EC-derived GPP, there was nonetheless very good agreement between GPP estimates derived from EC measurements (using the partitioning method of Reichstein et al., 2005), and those modelled by CenW, with model efficiencies of 0.79 and 0.84 for daily and weekly comparisons, respectively (Fig. 9). This included accurate modelling of the seasonal cycle, with low winter rates of about 30 kgC ha^{-1} d^{-1}, rising to early-summer peaks of about 120 kgC ha^{-1} d^{-1}. The lowest rates were obtained during the 2008 drought when rates fell to less than 10 kgC ha^{-1} d^{-1}. GPP also fell sharply during the summer of 2009 but, in that year, rainfall returned before drought conditions became too severe.

4. General discussion

The work reported here has shown that it was generally possible to obtain good agreement between measured and modelled CO_2 and H_2O fluxes in an intensively grazed pasture system. Agreement was particularly good for evapotranspiration rates, for which 91% of day-to-day variations and 96% of weekly variations could be explained by the model (Fig. 3). That included good capture of short-term variations due to variable weather conditions including rainfall that wetted the canopy, and normal seasonal variations between summer and winter caused by changing temperature and solar radiation. It also adequately captured the effect of drought conditions that occurred over both summers, but were most pronounced in 2008.

In previous work in a eucalypt forest, there had also been good agreement between observed evapotranspiration rates and those modelled by CenW (Kirschbaum et al., 2007). This consistent agreement suggests that the partitioning of evapotranspiration rates between surface evaporation, canopy evaporation and plant transpiration (see Lawrence et al., 2007) was realistic, and appropriately distinguished between the different drivers of evapotranspiration. The physically-based Penman–Monteith model (e.g., Wang and Dickinson, 2012) that is incorporated in CenW, coupled to GPP to provide changing stomatal conductance, especially during droughts, then provided a modelling approach to give modelled fluxes that were consistent with EC measurements.

CenW calculates stomatal conductance as a linear function of GPP and relative humidity (Ball et al., 1987). Other factors, such as solar radiation and temperature, were assumed to equally affect GPP and stomatal conductance. Plant water stress also affects both GPP and stomatal conductance, but may increase water-use efficiency under water-limited conditions (e.g., Korol et al., 1999). However, the data in the present experiment showed no discernible improvement in water use efficiency under drought conditions so that the relevant parameter was set to near-constant water use efficiency.

The data indicated that a limitation on plant function by soil water availability started when relative soil water contents fell below 77%, with plant function linearly impaired with further declining soil water contents. This fairly high threshold is even higher than a threshold determined in earlier work (e.g., Parfitt et al., 1985). Water availability at our experimental site fell below that threshold in each summer, which was most pronounced over the first season of the study. In other seasons, however, water limitations were not observed because of regularly recurring rainfall and lesser evaporative demand.

A good quantitative understanding of evapotranspiration rates is important for hydrological applications, such as modelling stream flow (e.g., McMahon et al., 2013), and how that might be modified by changing land cover (e.g., Brown et al., 2013) or environmental conditions (e.g., Gedney et al., 2006). Calculating evapotranspiration rates accurately is also useful for irrigation scheduling (Hedley and Yule, 2009) so that water applications can be targeted to times when pastures require extra water for optimum productivity while avoiding overwatering soils with limited water-holding capacity (Horne et al.,

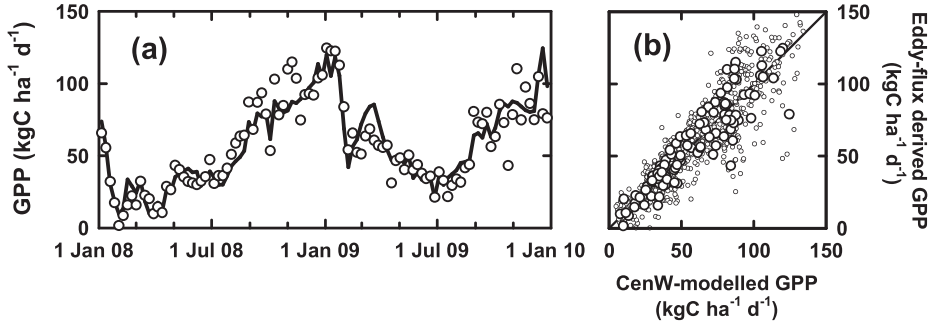

Fig. 9. Time course of estimated EC-derived (symbols) and CenW-modelled (solid line) weekly averaged GPP (a), and comparison of daily and weekly-averaged rates obtained by the two methods (b). Daily rates are shown with smaller symbols and weekly averaged rates larger with larger symbols. Model efficiencies for daily and weekly comparisons were 0.79 and 0.84, respectively. EC-derived rates were calculated from EC observations by the partitioning method of Reichstein et al. (2005).

Table B1
Main parameters used in the simulations of pasture productivity.

Parameter description	Parameter values	Units
Minimum foliage turn-over	0.027	yr^{-1}
Fine-root turn-over	2.21	yr^{-1}
Low-light senescence limit	0.05	MJ m^{-2} d^{-1}
Max daily low-light senescence	0.018	% d^{-1}
Max drought foliage death rate	5.65	% d^{-1}
Drought death of roots relative to foliage	0.086	–
Mycorrhizal uptake	0.01	g kg^{-1} d^{-1}
Soil water stress threshold (W_{crit})	0.736	–
Respiration ratio per unit N	0.566	–
beta parameter in T response of respiration	2.09	–
Temperature for maximum respiration	49.5	°C
Growth respiration	0.3	–
Time constant for acclimation response of respiration	196	d
Relative temperature dependence of heterotrophic respn	0.545	–
Specific leaf area	19.8	m^2 (kg DW)$^{-1}$
Foliage albedo	5.7	%
Transmissivity	1.9	%
Loss as volatile organic carbon	0	%
Threshold N concentrations (N_o)	5.2	gN (kg DW)$^{-1}$
Non-limiting N concentration (N_{sat})	40.0	gN (kg DW)$^{-1}$
Light-saturated maximum photosynthetic rate (A_{max})	41.1	μmol m^{-2} s^{-1}
Maximum quantum yield	0.06	mol mol^{-1}
Curvature in light response function	0.515	–
Light extinction coefficient	0.79	–
Ball–Berry stomatal parameter (unstressed)	8.7	–
Ball–Berry stomatal parameter (stressed)	8.0	–
Minimum temperature for photosynthesis (T_n)	−3.0	°C
Lower optimum temperature for photosynthesis ($T_{opt,\ lower}$)	15.9	°C
Upper optimum temperature for photosynthesis ($T_{opt,\ upper}$)	25.3	°C
Maximum temperature for photosynthesis (T_x)	39.2	°C
Temperature damage sensitivity (s_T)	0.02	–
Threshold for frost damage	0.4	°C
Water-logging threshold (L_{log})	0.994	–
Water-logging sensitivity (s_L)	8.9	–
Ratio of [N] in senescing and live foliage	0.84	–
Ratio of [N] in average foliage to leaves at the top	0.69	–
Foliar lignin concentration	10.0	%
Root lignin concentration	15.0	%
Atmospheric N deposition	2.0	kgN ha^{-1} yr^{-1}
Biological N fixation	4.0	gN kgC^{-1}
Volatilisation fraction	10	%
Leaching fraction	0.49	–
Litter water-holding capacity	2.0	g gDW^{-1}
Mulching effect of litter	2.8	% tDW^{-1}
Canopy aerodynamic resistance	87	s m^{-1}
Canopy rainfall interception	0.04	mm LAI^{-1}
Maximum rate of soil evaporation	1.45	mm d^{-1}
Fine soil proportion	54	%
Organic matter transfer from surface to soil	90	% yr^{-1}
Critical C:N ratio	10	–
Decomposition rate adjustment	0.81	–
Ratio of C:N ratios in structural and metabolic pools	5.0	–
Exponential term in lignin inhibition	5.0	–
Water stress sens. of decomp. relative to plant processes	0.53	–
Residual decomposition under dry conditions	0.05	–
Mineral N immobilised	5.6	% d^{-1}
Allocation to reproductive organs	None	–
Fine root: foliage target ratio (nitrogen-unstressed)	0.96	–
Fine root: foliage target ratio (nitrogen-stressed)	1.86	–
Used target-oriented dynamic root-shoot allocation	Yes	
Fine root:foliage [N] ratio	0.82	–
Growth K_m for carbon	1.8	%
Growth K_m for nitrogen	2.1	%
Drop of standing dead leaves	0.7	% d^{-1}
Decomposability of standing dead relative to metabolic litter	1.0	–

2011). Soils can hold only certain amounts of soil water, and especially for some shallow soils, the amount of available soil water can be quite limiting for plant growth. If soils receive too much irrigation water, the excess can drain beyond the root zone and be wasted. If they receive insufficient irrigation water, plant productivity and farm incomes will be reduced. Accurate modelling of evapotranspiration can thus ensure that irrigation applications meet plant requirements without exceeding them.

NEP could not be modelled with the same accuracy as evapotranspiration rates, although agreement was still considered adequate. NEP is the balance between CO_2 uptake through GPP and CO_2 loss through TER. Of those, GPP was modelled well, with good description of seasonal

variations and the effect of drought conditions (Fig. 8). In CenW, the calculation of GPP is explicitly linked to various physiological processes (see Kirschbaum, 1999). The most important ones for the present work were dependencies on light interception and its reduction through grazing-induced reduction of available leaf area, and temperature and soil moisture modifiers, which were empirically fitted against the observational data.

The largest uncertainty in NEP modelling related to the correct capture of respiratory CO_2 losses during grazing events. Our experimental site posed particular challenges in this regard as it consisted of 26 small paddocks that each followed their own grazing and harvesting patterns. We used the available grazing records, which allowed consistent modelling of fluxes for the majority of days when there were no grazing events on the four inner paddocks. However, even with explicit inclusion of all recorded grazing events, there was still incomplete agreement between modelled and observed night-time NEP when cows grazed the paddocks immediately around the EC tower (Fig. 6). This could have been related to problems in either the modelling or the measurements.

Good agreement between measured and modelled NEP could be achieved when days were excluded that had grazers present on the four inner paddocks. To achieve good agreement with observations also required explicit modelling of the gas exchange of each paddock within the footprint area of the tower. These individual fluxes were then combined using a footprint model to estimate the combined flux at the tower, which provided the appropriate comparison against observed fluxes. This approach worked in our system despite some large variations in fluxes when winds shifted between grazed and non-grazed paddocks.

Footprint modelling of EC data is an on-going field of investigation, and there are a number of models with varying complexity that may be applied to different situations (Rannik et al., 2012). Marcolla and Cescatti (2005) specifically tested different footprint models over a spatially heterogeneous meadow and found that the Kormann and Meixner (2001) model generally performed well when compared to observations. This model is also commonly used by other researchers working over short vegetation like crops and grasslands (e.g., Ammann et al., 2007; Davis et al., 2010; Dengel et al., 2011), and we therefore used it for our work as well. Inclusion of a footprint model to apportion modelled fluxes was an important component that improved the agreement between modelled and observed data (data not shown).

The footprint model indicated that, while most of the flux footprint was related to activities in the four paddocks immediately surrounding the tower (Fig. 1), the outer paddocks could also make substantial flux contributions on specific days. Over the 2 years of the experiment, 17% of daytime and 30% of night-time fluxes even originated from outer areas beyond the 26 paddocks that were explicitly modelled (Fig. 1). It is therefore possible that grazing events on specific outer paddocks could have also contributed unexpected large respiration fluxes on some days.

Comparison between averaged and footprint-weighted CO_2 exchange rates showed that there could be considerable differences (Fig. 7; Table 2) in fluxes expected at the EC tower. These differences were primarily related to the appropriate capture of grazing events (Table 2), and weighting of modelled fluxes by the footprint model could considerably improve the agreement between observed and modelled CO_2 fluxes. To achieve good agreement between modelled and observed data, it is therefore essential for such a weighting of fluxes to be applied.

One must presume that grazing by large herds of cows in only some of the paddocks surrounding the EC tower, as was the case at our experimental site, caused non-stationary CO_2 concentrations and fluxes as the flux footprint traversed strongly contrasting surface sinks and sources brought about by grazing animals. This would have violated one of the key requirements for high quality EC measurements. Tests for stationarity can include filters like that described by Foken and Wichura (1996), or filters like the ones used in this study which rejected fluxes obtained at times with high standard deviations of measured CO_2 density, or CO_2 fluxes that deviated too strongly from mean fluxes measured at corresponding periods in other years.

Several researchers have assumed that animal respiration could be adequately measured by EC systems (e.g., Jaksic et al., 2006; Byrne et al., 2007; Soussana et al., 2007). In contrast, Skinner (2008), who measured CO_2 fluxes over pastures in Pennsylvania, found that during grazing events, flux data were 'extremely erratic and variable', which he attributed to the close proximity of animals to the EC system at times of grazing, high stocking rates, and the short duration of grazing episodes. In addition, Zeeman et al. (2010) argued that animal respiration could probably only be measured reliably by EC techniques if cows are spread evenly over the paddocks at all times. After examining methane fluxes over a peatland in great detail, Baldocchi et al. (2011) also advised caution when interpreting EC measurements of CH_4 and CO_2 made while animals graze the flux source area. Full capture of grazing events also remained incomplete in our study (e.g., Fig. 6), and it is not realistic to expect that grazing fluxes could be captured completely.

Our findings suggest that researchers measuring CO_2 fluxes in a rotationally grazed pasture need to consider the problem of respiration by grazing animals when large numbers of animals graze over a substantial portion of the flux footprint. If data collected on such days are rejected, there are then three options for filling the gaps:

1) Only use data collected when there were no cows in the footprint area and thereby completely ignore the respiration by grazing animals. This would be appropriate if the main research question focused exclusively on the CO_2 exchange between the pasture + soil system and the atmosphere (e.g., Skinner, 2008), but overall NEP would be biased by the missing emissions during grazing events.
2) Use estimates of the net CO_2 exchange including respiration by grazing herbivores, including estimates of pasture cover before and after grazing, and the percentage of C intake respired by herbivores (e.g., Zeeman et al., 2010). This then needs to be weighted by the contribution of the grazed paddocks to the measured EC flux during the grazing event using output from a footprint model. This latter approach is appropriate when aiming to quantify the net ecosystem carbon balance of the footprint area.
3) Use a stand-alone model to simulate all aspects of pasture gas exchange, including plant and soil processes and independently estimate the contribution from grazer respiration. The model can be parameterised against observations when they are considered to be reliable, and then use the model to fill any gaps with unreliable data and to generate long-term NEP sums.

The present work confirmed that CenW is an appropriate tool to model the water vapour and CO_2 fluxes of a grazed pasture system under different conditions. It can thus be used to assess the carbon storage implications of using alternative management options, or to assess the effect of climatic changes on soil carbon stocks. Changes in soil organic carbon stocks under changing land management involve intricate interactions between plant productivity, animal carbon off-take and resultant feedbacks on plant productivity (e.g., Conant et al., 2001; Parsons et al., 2013). In order to assess net effects on soil carbon stocks, it is thus necessary to employ comprehensive modelling approaches that can independently quantify these different interacting processes for net effects on carbon stocks. CenW can be used in future work to quantify the net effects of different management options for soil organic carbon storage.

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Appendix A. New simulation routines used in CenW

A.1. Dynamic allocation to roots and leaves

In previous work, the allocation of carbon and nitrogen to different biomass components was varied based on plant-internal factors, especially plant nutrient status (Kirschbaum, 1999), but it was not related to the existing sizes of respective biomass pools. That causes anomalies, however, when the sizes of leaf and root pools undergo major changes due to factors that are not related to the allocation of new carbon to new biomass, such as through grazing. When the ratio of roots to leaves is thus elevated through these extra factors, it was considered appropriate that further carbon and nitrogen allocation should not follow the same allocation ratios that might have been appropriate without the extra perturbations. Instead, we assumed that plants allocate new growth to the organs that have been depleted through external factors (i.e., preferentially allocate new growth to foliage after grazing).

The carbon allocation ratio between fine roots and foliage, $a_{r,a}$, was thus modified to:

$$a_{r,a} = a_{r,adj} a_{rt}/(a_{rt}+1) \tag{1a}$$

$$0.01 < a_{r,\ a} < 0.99 \tag{1b}$$

where $a_{r,\ a}$ and $a_{r,\ t}$ are the actual and target root:leaf allocation ratios, and $a_{r,adj}$ is an adjustment term that shifts the root:leaf allocation of new growth towards their target values.

The adjustment term $a_{r,\ adj}$ is calculated as:

$$a_{r,\ adj} = 1/\exp\left(-10 a_{r,\ dev}\right) \quad \text{if} \quad a_{r,\ dev} > 0 \tag{2a}$$

$$a_{r,\ adj} = \exp\left(10 a_{r,\ dev}\right) \quad \text{if} \quad a_{r,\ dev} < 0 \tag{2b}$$

$$a_{r,\ adj} = 1 \quad \text{if} \quad a_{r,\ dev} = 0 \tag{2c}$$

where $a_{r,\ dev}$ is a measure of the difference between target and actual root:leaf ratios, calculated as:

$$a_{r,\ dev} = a_{r,\ targ} - \mathrm{R/L} \tag{3}$$

where $a_{r,\ targ}$ is the target root:leaf ratio and R and L are the actual amounts of carbon in the root and leaf pools, respectively.

The new routine first works out a target root:leaf ratio based on set parameters and plant nutrient status as was done previously (Kirschbaum, 1999). The actual allocation ratio is then adjusted based on the difference between the target allocation and the current root:leaf ratio. After grazing, in particular, the root:leaf ratio is temporarily increased, and new carbon is preferentially allocated to new leaf growth until the actual root:leaf ratio reaches the target ratio again.

A.2. Growth limit during water stress

Growth slows down under conditions of water stress. A new term has been added to provide greater scope to describe the extent of that growth limitation, G_w, under water stress.

$$G_w = W_{lim}^{x_w} \tag{4}$$

where W_{lim} is a water-stress limitation term (0..1) and x_w is an exponent that describes the severity with which water stress reduces growth and conserves carbohydrate resources. These carbohydrate resources then allow faster recommencement of high growth rates at the end of any drought period.

Water limitation is calculated for each layer as:

$$W_{lim,j} = \left(W_j/W_{hold,j}\right)/W_{crit} \quad \text{if} \quad \left(W_j/W_{hold,j}\right) < W_{crit} \tag{5a}$$

$$W_{lim,j} = 1 \quad \text{if} \quad \left(W_j/W_{hold,j}\right) \geq W_{crit} \tag{5b}$$

where W_j is the amount of water held in each soil layer, $W_{hold,\ j}$ is the water holding capacity of that layer, and W_{crit} is an empirical term that determines the relative water content when water stress begins to impair plant function. These values for individual layers are then combined to calculate an overall limitation as:

$$W_{lim} = \sum s_{w,j} W_{lim,j} \tag{6}$$

where $s_{w,\ j}$ is the relative contribution of each soil layer towards determining the overall water-stress sensitivity. The sum of all relative contribution terms for all soil layers must be 1 by definition.

A.3. Standing dead biomass

When foliage dies it can either fall onto the soil surface and become part of the decomposing litter pool, or remain standing for some time where it either decomposes during wet periods while still standing, or eventually falls onto the soil surface either by just falling down or being trampled by cattle. It was important to model these processes as the estimates of foliage biomass included a component of dead standing biomass that was not separated out in the data. These processes were modelled by assuming that all senescence, or drought-induced leaf death, initially transferred foliage from a live to a dead-foliage pool. The rate of loss from the dead foliage pool, dL_d/dt, was described as:

$$dL_d/dt = f_d L_d + k_s f(T)\ \left(1-l_f\right) L_d \quad \text{if foliage is wet} \tag{7a}$$

$$dL_d/dt = f_d L_d \quad \text{if foliage is dry} \tag{7b}$$

where L_d is the pool of standing dead biomass, f_d is the daily proportion of dead foliage falling to the ground, k_s is a decomposition rate constant, l_f is the lignin fraction of foliage, and $f(T)$ is the same temperature response function that also describes the temperature dependence of organic matter decomposition.

It was also assumed that cattle preferentially grazed live foliage, but that they include an increasing proportion of dry foliage in their intake as the proportion of dry foliage in total foliage increases. This was calculated as:

$$g_a = \frac{g_l + (g_h - g_l) e^{-0.5(1-f_l)}}{g_l} \tag{8}$$

where g_a is the fraction of live foliage that is grazed, g_l and g_h are the lowest and highest fractions of live foliage that could possibly be ingested and f_l is the proportion of all foliage that is alive. The highest and lowest fractions of live foliage that could be grazed were calculated as:

$$g_l = 0 \quad \text{if} \quad (1-f_l) > g_t \tag{9a}$$

$$g_l = g_t[1-(1-f_l)/g_t] \quad \text{if} \quad (1-f_l) <= g_t \tag{9b}$$

$$g_h = g_t \quad \text{if} \quad f_l > g_t \tag{10a}$$

$$g_h = f_l \quad \text{if} \quad f_l <= g_t \tag{10b}$$

where g_t is the total fraction of biomass grazed during a grazing event.

Appendix B. Parameters for pasture simulations

The key parameters and processes for CenW simulations have been described by Kirschbaum (1999). The model was further developed by including a number of new modelling routines, which are described in Appendix A. The final parameterisation to obtain the best description of the present data set is provided in Table B1. Most parameters were optimised against the observations as described, but the following parameters were prescribed based on prior observations. The parameters for the volatilisation fraction during N mineralisation (10%), organic matter transfer from the surface to the soil (90% yr^{-1}), the critical C:N ratio for N mineralisation (10), the ratio of C:N ratios in structural and metabolic pools (5), foliar and root lignin concentrations (10 and 15%, respectively), and the exponential term in lignin inhibition of structural litter decomposition (5) were based on prior work with CenW (Kirschbaum et al., 2008). Critical foliar nitrogen concentration was set to 40 gN $(kgDW)^{-1}$ based on Lamb et al. (2002) and Sanches et al. (2013). Biological nitrogen fixation was set to 4.0 gN kg C^{-1} to obtain observed maximum N fixation rates under conditions of N limitation (e.g., Ledgard et al., 2009).

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